GAMBUSIA HETEROCHIR, A NEW POECILIID FISH FROM TEXAS, WITH AN ACCOUNT OF ITS HYBRIDIZATION WITH *G. AFFINIS*

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During the past decade a number of fishes have been described from Texas fresh-waters. Some of them have been known for years, but were not described until recently. Others, such as the new species of *Gambusia* described below, have not been recognized until recently. This new mosquitofish, apparently restricted to the headwaters of Clear Creek, Menard County, Texas, is separated by some 800 miles from the ranges of its nearest relatives.

Many hybrids between this species and *Gambusia affinis* (Baird and Girard) have been collected. The geographic distribution and morphologic variation of the hybrids is discussed.

Material of the new species has been collected by the author, W. Gordon Craig, Theodosius Dobzhansky, Alvin E. Ellington, Sr., James D. French, Murray K. Muston, Kirk Strawn, and John E. Tilton. I also wish to thank Charles Wilkinson and H. Leslie Jones for permission to collect on their ranches. Dr. Billie L. Turner identified the plants. Mr. George G. Henderson, Jr., made the photographs. Miss Nancy Walker and Mrs. Jane Hubby made the drawings. Counts and measurements were made as detailed in Carl L. Hubbs and Lagler (1947). Names for gonopodial structures follow those given by Carl L. Hubbs (1926). The schematic diagrams to determine degree of hybridization are modified from those proposed by Anderson (1949).

GAMBUSIA **HETEROCHIR**, sp. nov.

Fig. 1

Material.—The type material consists of the 24.5 mm holotype (University of Michigan Museum of Zoology No. 170936) and 125 other specimens of 17 to 45 mm (UMMZ No. 170937, Stanford University Nos. 46445 to 46451, United States National Museum No. 164573, Museum of Comparative Zoology, Harvard University No. 39684, Chicago Natural History Museum No. 61805, and Texas Natural History Collection Nos. 3065 and 4652), all of which were seined on two occasions from the headspring of Clear Creek, Menard County, Texas, 10.4 miles west of Menard. The first of these collections was made on February 22, 1953, and the second on February 20, 1956.

Many hybrids with *G. affinis* occur in both collections. Possibly some or all of the specimens designated as *G. heterochir* contain some genes from *G. affinis*. However, as introgression into *G. heterochir* appears to be uncommon and suspected hybrids are excluded from *G. heterochir* collections, I believe that most of the specimens considered to be *G. heterochir* are not contaminated with *G. affinis* genes.

Diagnosis.—A stocky species of *Gambusia*. The deep indentation on the upper margin of the male pectoral fin (fig. 5) distinguishes

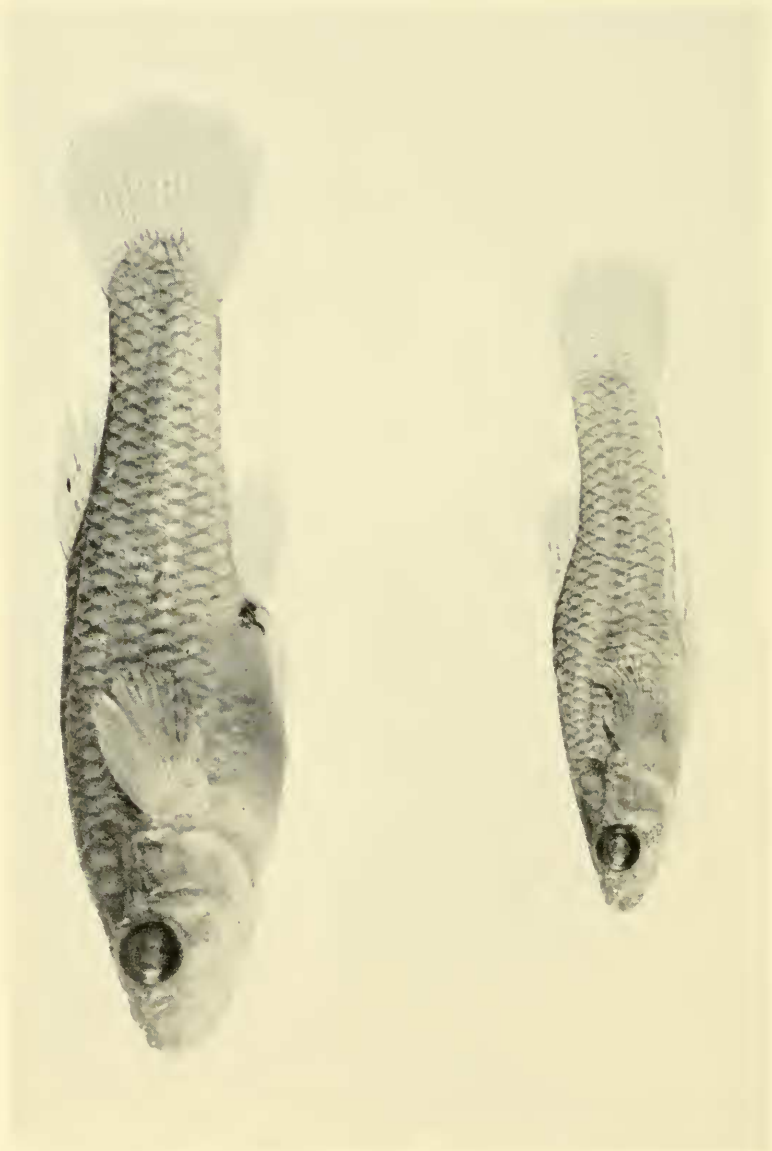

Figure 1. *Gambusia heterochir*, sp. nov. Left: 33 mm female; Right: 23 mm male; both from TNHC 4652.

G. heterochir from all known gambusiine species. It also has the largest gonopodial elbow and bluntest gonopodial tip (fig. 3) when compared with the other known gambusiines.

Description.—A minimum of ten adult males and ten adult females were used for the descriptions. Up to 86 specimens were examined for characters used in the analysis of hybridization. Fin rays: dorsal 7 or 8 (rarely 9); branched caudal 14 (rarely 13 or 15); anal 9 (rarely 10); pelvic 6 (rarely 5); pectoral 13 to 15. Scales: lateral line 30 or 31; caudal peduncle 16; predorsal rows 15 or 16.

The bluntly rounded head enters (step-measurement) standard length 3.7-3.8 times in adult males and 3.3-3.7 times in adult females. The depth at the back of the eye slightly exceeds the width. The gape is equal to or slightly exceeds the snout length. The head is scaled to the anterior margin of the eye. The anterior nostrils open at the posterior lip of the premaxillary groove; the posterior ones open dorsal and anterior to the eye. The lateral line pits on the head are more or less connected: a single large pit mesial and anterior to the posterior nostril; two connected mesial and posterior to the posterior nostril; a crescent shaped series posterior to the upper margin of the eye; a connected row on the posterior margin of the preopercle; an interrupted series of pits on the ventral margin of the preopercle and the mandible; and a connected series of small pits in front of the eye.

The body is deep and rounded. The highest point on the dorsal profile is at or immediately anterior to the anterior dorsal base. The distance between the dorsal insertion and the posterior end of the hypural plate is contained 1.2 to 1.3 and 1.4 to 1.7 times in the predorsal length of males and females respectively.

The dorsal fin is rounded, its depressed length is contained 3.9 to 4.3 and 4.3 to 4.9 times in the standard length of males and females respectively. The caudal is rounded. The anal of females is rounded, that of males modified into a gonopodium. The pelvics are small and the inner ray is bound to the abdomen by a membrane. The pectoral is rounded, the sixth and seventh rays the longest.

The gonopodium of males is distinctive (fig. 3). The anterior branch of ray four reaches almost to the tip of the gonopodium. The two- to four-segmented elbow is longer than the longest modified spine of ray three and often overlaps the adjoining unmodified segments of ray three. The distal serra on the posterior branch of ray four is distal to the elbow. The serrae are numerous and long. The terminal hook is pointed at the distal tip. The terminal hook on the anterior branch of ray five is rounded. The distal segments of that ray meet the main axis of the gonopodium at an angle of more than 45°. Similar to other members of the *G. nicaraguensis* species group, the modified spines on ray three are sharply distinguished from the more proximal undifferentiated segments and the length of the longest spine is much less than the combined basal lengths. One or two of the proximal modified spines have recurved hooks.

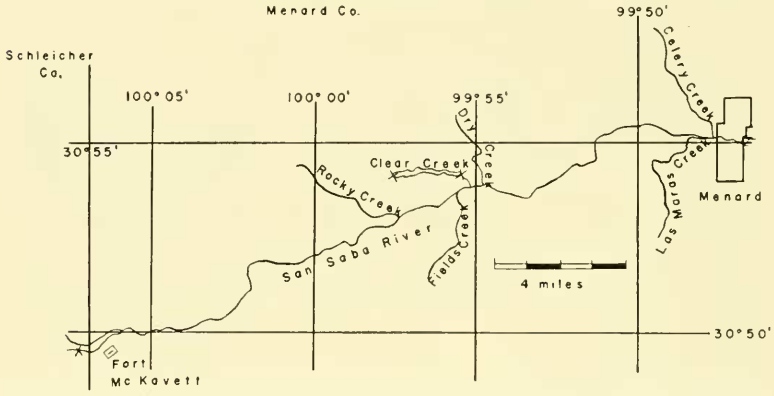

Figure 2. Map of the Clear Creek region. Collection localities designated by "X". *G. heterochir* known only from headwaters of Clear Creek.

Both pectorals of the males are modified. Rays two through five have a flattened region along the ray. The inner half of the ray does not enter into the flattened blade of rays three through five. The upper margin has a deep incision near its tip. Apparently this incision is to steady the gonopodium during intromission.

The color pattern is distinctive. The midorsal coloration is not darker than that of the adjacent area; *i.e.*, there is no middorsal stripe. A fine axial streak extends from the midline above the anus to the caudal base; however, there is no diffuse lateral band surrounding the axial streak. The subterminal dusky markings on the body scales are absent only on the abdominal scales. A large number of the subterminal dusky marks are darker and form black crescents, which are found on all but the predorsal scales. The fine postanal streak is darker than the adjacent subterminal dusky scale marks. In adult females the large black crescents, which extend on each side from in front of the anus to behind the anal origin, do not meet across the midventral line. These anal marks are absent in young and in adult males. The head ground color is similar to that of the body. A black mark at the upper corner of the opercle covers more than one scale. The weak suborbital bar does not reach to the corner of the preopercle. The lips are no darker than the adjoining parts of the head. The dark lateral line pits on the head have light edges. The dorsal has a median row of dark spots and the other fins are dusky to colorless.

Relationships.—In his review of the genus *Gambusia*, Carl L. Hubbs (1926) divided the genus into four subgenera (*Heterophallina* Hubbs, *Gambusia* Poey, *Arthrophallus* Hubbs, and *Schizophallus* Hubbs). Krumholtz (1948) stated that Hubbs and Walker (unpublished ms) consider that two nominal species (*affinis* and *holbrooki*), comprising the nominal subgenera *Arthrophallus* and *Schizophallus* respec-

tively, regularly intergrade in nature and therefore are to be assigned to the same species. Carl L. Hubbs (1929) divided the subgenus *Gambusia* into two species groups, *nobilis* and *nicaraguensis*, and reviewed the former. In his 1926 paper he separated the species comprising the two species groups by key item "h". Members of the *G. nicaraguensis* group differ from those in the *G. nobilis* group in that the former have (1) shorter distal spines on ray three of the gonopodium, (2) the dusky lateral band indistinct or developed only on the trunk, and (3) no dark markings on the anal. *Gambusia heterochir* has the shorter distal spines on the third gonopodial ray and the dusky lateral band indistinct. In both characters it resembles the *G. nicaraguensis* species group. The females have the dark anal markings characteristic of the *G. nobilis* species group. I consider

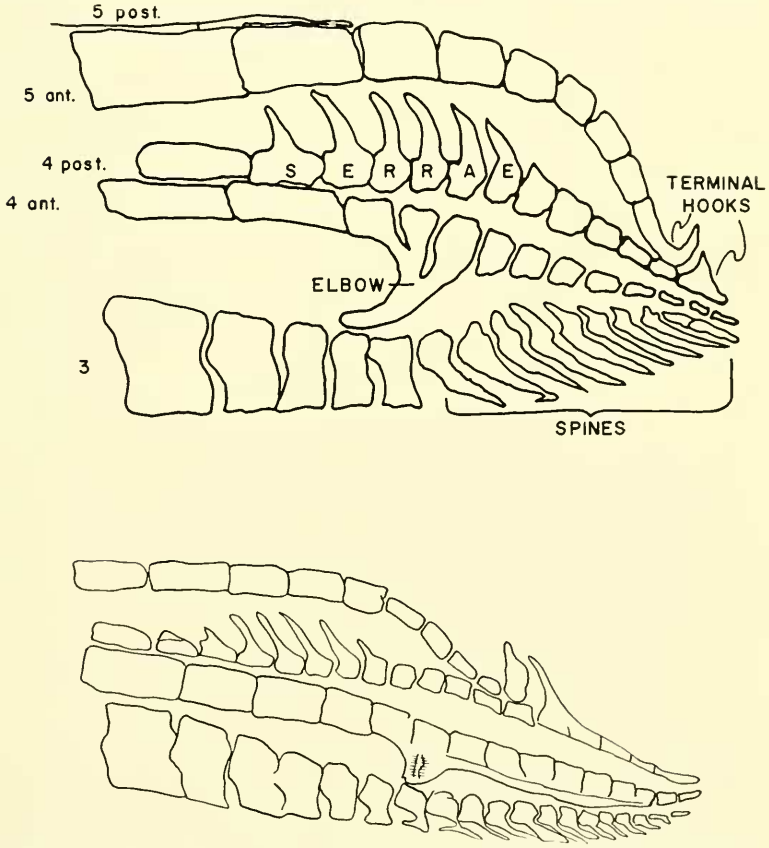

Figure 3. Camera lucida drawings of gonopodial tips: **A** (upper), *G. heterochir* from type locality; **B** (lower), *G. affinis* from Middle Valley Prong of San Saba River.

that *G. heterochir* evolved from the ancestral stock of *G. nicaraguensis* shortly after that stock separated from the ancestral stock of *G. nobilis.*

Range.—*Gambusia heterochir* is known only from the headsprings of Clear Creek, Menard County, Texas, 10.4 miles west of Menard (fig. 2) and from one locality near the shore 350 yards east of the headsprings. Many other collections have been made in headwaters of the San Saba River in Menard and Schleicher counties, covering all known habitats and concentrating on habitats similar to that of the headsprings of Clear Creek. One of the collections is from the lower part of Clear Creek. None of these collections contains *Gambusia heterochir.* I believe that *G. heterochir* once had a wide distribution in Central Texas. Its range probably has been restricted because this species is unable to compete with *G. affinis.* Clark Hubbs and Springer (ms) suggest that members of the *G. nobilis* species group have restricted ranges for the same reason.

Ecology.—The headsprings of Clear Creek are now impounded. The upper and lower of three dams enclose a small body of water, the middle impounds the bulk of the water. Except for the upper reservoir and the adjacent part of the middle reservoir, the banks are covered with cattails. The collections were made in the cattail-free areas. Submerged and emergent vegetation was prolific in all impounded parts of Clear Creek. A dense growth of *Ceratophyllum* sp. occurred in the headspring. A species of *Ludwigia* was found with the *Ceratophyllum.* Another *Ceratophyllum* bed occurred where the *G. heterochir* was sampled 350 yards east of the headspring. A dense stand of *Jussiaea* sp., *Distichlis* sp., *Typha latifolia,* and *Hydrocotyle umbellata ?* also were found there. Dense growths of *Myriophyllum* sp., *Potomogeton* spp., *Chara* sp., and *Conium maculatum* occurred elsewhere, but no *G. heterochir* specimens were collected. I suspect that *G. heterochir* populations were correlated with factors that were associated with *Ceratophyllum* beds. Daytime surface water temperatures varied between 18.3 and 20.6° C in February and between 27.0 and 31.0° C in July. Although temperatures near 21° C occurred at the bottom (6 inches below the surface) at both seasons, this probably had little effect on the fish as they remained on the surface unless disturbed. Night temperatures were probably lower than those taken during daylight hours.

The name *heterochir* is derived from the Greek *heteros* (= different) and *cheir* (= hand) for the distinctive shape of the pectoral fin.

Hybridization with *Gambusia affinis*

In his account of natural hybridization in poeciliid fishes, Carl L. Hubbs (1955), listed only two hybrid combinations in the genus *Gambusia:* between two members of the *G. nicaraguensis* species group and between *G. nobilis* and *G. affinis.* The hybrids discussed below constitute a third example, and are the first documented record of natural hybridization amongst gambusiines.

The collections contain specimens of *G. heterochir, G. affinis,* and

hybrids. The hybrids do not constitute a discrete intermediate group as described by Carl L. Hubbs, Hubbs, and Johnson (1943) for natural F_1 hybrids, but definitely grade into *G. affinis* and may grade into *G. heterochir*. Thus it appears likely that F_2 and or back crosses occur in the Clear Creek population and gene flow occurs between the two species. However, Clark Hubbs and Strawn (in press) and Clark Hubbs (1956) report F_1 hybrids that are not always intermediate between their parental types. As the two parental species are included in different subgenera, the hybrids are easily recognized and a study of the hybrid swarm may be of value in the study of the selective advantages of hybrids.

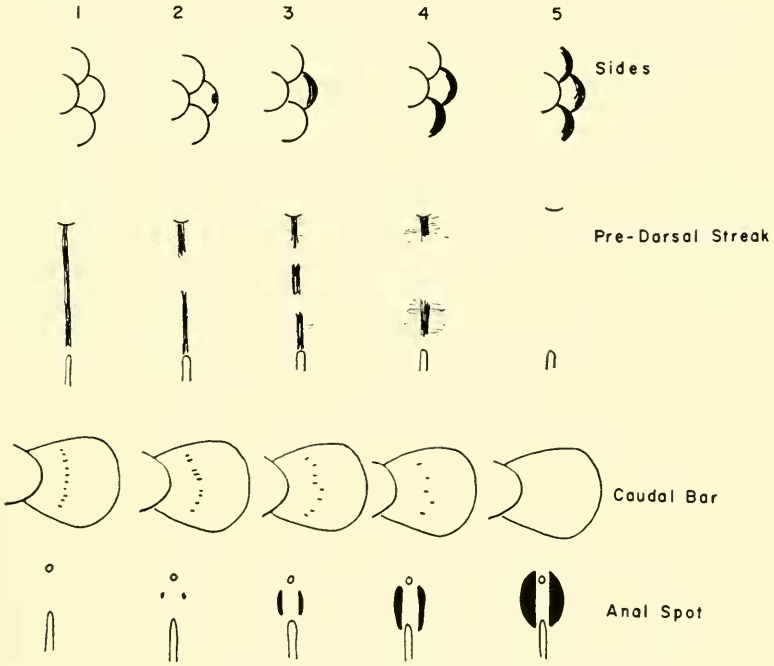

Figure 4. Color codings for individuals in hybrid swarm. Lower numbers for *G. affinis*, higher for *G. heterochir*, intermediate for hybrids.

All of the *Gambusia* specimens in four collections have been analyzed. The collections are: two from the headwaters of Clear Creek; one from the lower part of Clear Creek, 2.4 miles downstream from the hybrid swarm; and one from Middle Valley Prong of the San Saba River, 1 mile west of Ft. McKavett, 17 stream miles from the hybrid swarm. The two collections from the hybrid swarm were selected for obvious reasons. The Middle Valley Prong collection is typical of

G. affinis populations in the area, contains many specimens, and is from a locality ecologically similar to the headwaters of Clear Creek. This collection should show the morphology of uncontaminated *G. affinis*. The collection from the lower reaches of Clear Creek was analyzed to determine if the introgressed population extends downstream.

The data from these four collections have been graphed (figs. 6, 7) following the techniques proposed by Anderson (1949). As poe-

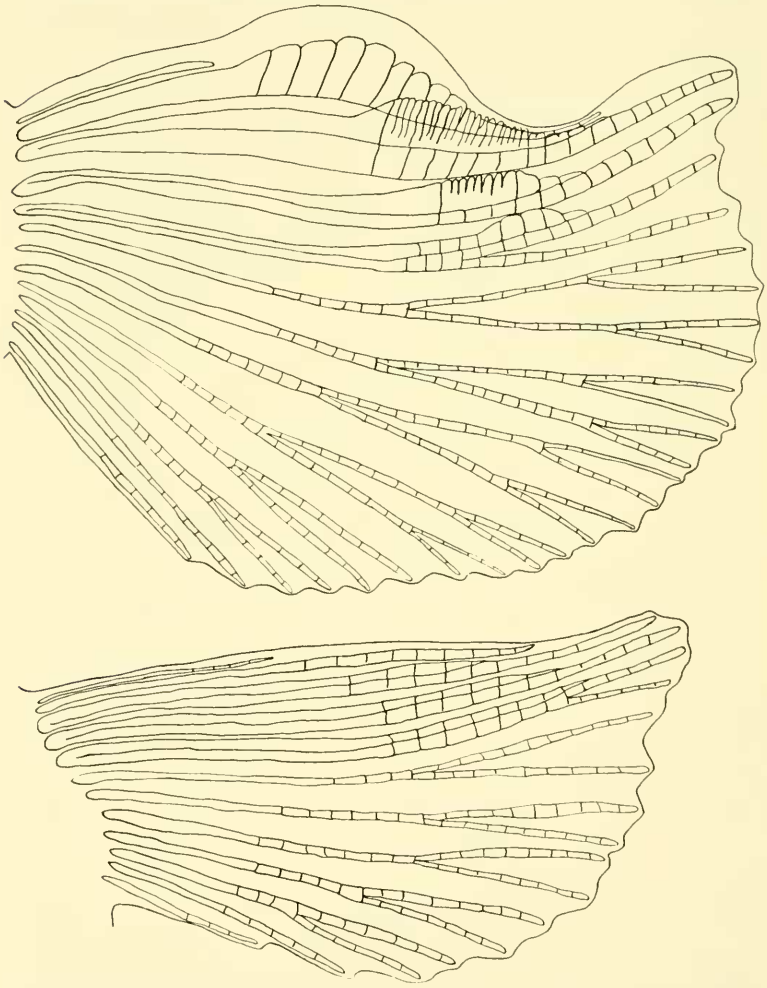

Figure 5. Pectoral fin structure of male: **A** (upper), *G. heterochir*, from a 20 mm specimen from type locality; **B** (lower), *G. affinis*, from a 22 mm specimen from Middle Valley Prong of San Saba River.

ciliids exhibit marked secondary sexual dimorphism the sexes are plotted separately. Only mature males are used since immature males approach females in many characteristics. Only females over 25 mm (standard length) are graphed because some color characteristics are not established until that size. For both sexes the ordinate is the head width added to the head depth (both at the back of the eye) divided by the standard length. The figures do not change appreci-

Figure 6a. Pictorialized scatter diagram of *Gambusia* males (see text for explanation of coding). Samples from headwaters of Clear Creek.

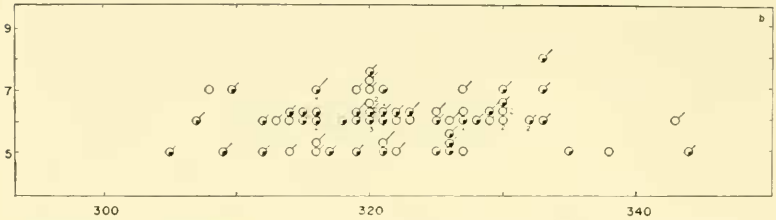

Figure 6b. Pictorialized scatter diagram of *Gambusia* males (see text for explanation of coding). Sample from Middle Valley Prong of San Saba River.

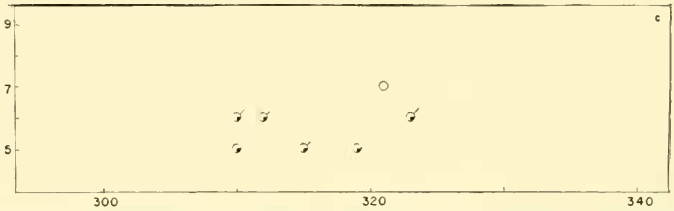

Figure 6c. Pictorialized scatter diagram of *Gambusia* males (see text for explanation of coding). Sample from lower part of Clear Creek.

ably in females over 25 mm standard length. In this index *G. heterochir* figures exceed those of *G. affinis*, and female figures exceed those of males. Environmental factors may effect meristic and morphometric characters of *Gambusia* species during development (Clark Hubbs and Springer, ms.). However, fish from the same locality probably are subjected to similar environmental factors during development. The minor differences between the figures for different populations may in part be due to different environmental factors acting during development; however, in so far as possible sample localities were selected that had similar environments. The abcissa of the graphs for males is made up of the sum of five gonopodial characters that were tabulated from one to five, with the lower numbers for *G. affinis* morphology. The two parental types are shown in Figure 3. The gonopodial characters are: the number of segments in the terminal hook on the posterior branch of ray four; the relative location of the terminal serra of the posterior branch of ray four when compared with the location of the elbow on the anterior branch of ray four; the structure of the elbow; the number and length of the modified spines on ray three; and the angle of contact of the anterior branch of ray five with the main axis of the gonopodium. The abcissa of the graphs for females is made up of the sum of four color characters, that were tabulated from one to five, with the lower numbers for *G. affinis* colors. The color codings are shown by Figure 4. The number of dorsal rays for both sexes is shown by the amount of shading within the circle: no shading = 5 rays; one-quarter shaded

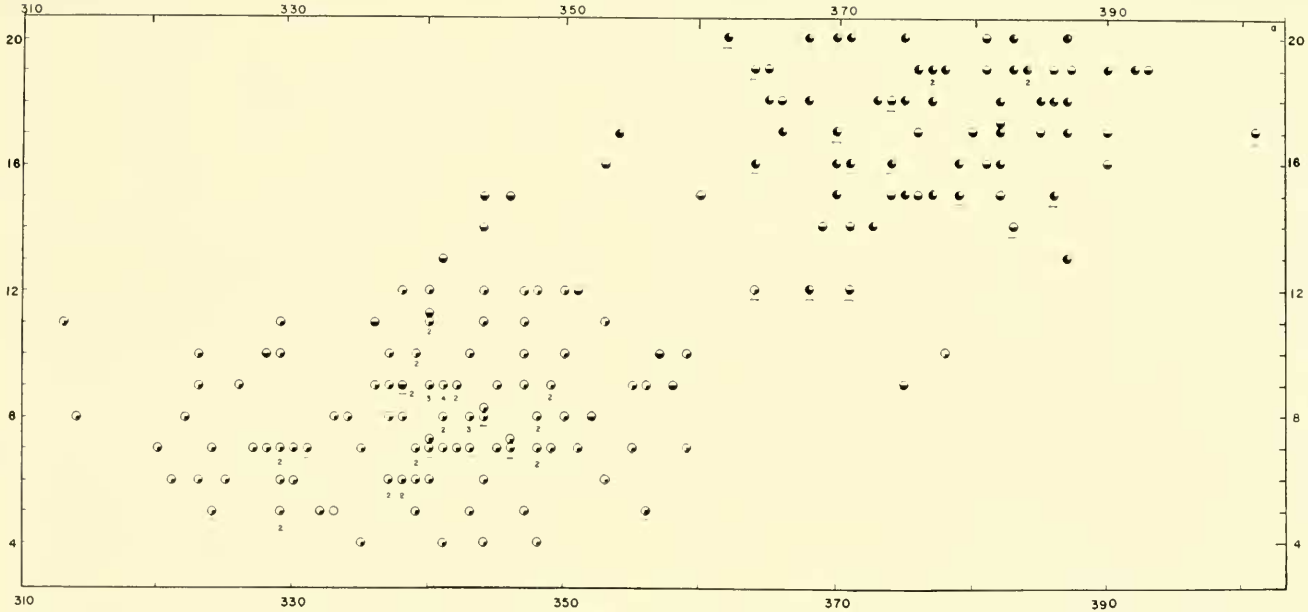

Figure 7a. Pictorialized scatter diagram of *Gambusia* females (see text for explanation of coding). Samples from headwaters of Clear Creek.

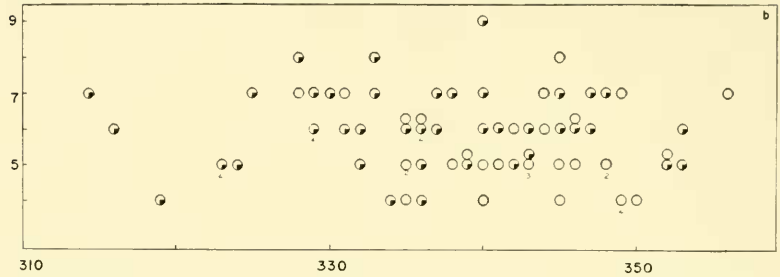

Figure 7b. Pictorialized scatter diagram of *Gambusia* females (see text for explanation of coding). Sample from Middle Valley Prong of San Saba River.

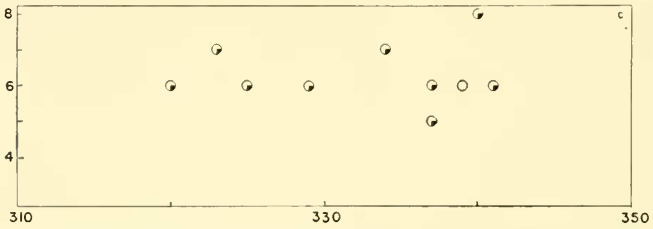

Figure 7c. Pictorialized scatter diagram of *Gambusia* females (see text for explanation of coding). Sample from lower part of Clear Creek.

= 6 rays; one-half shaded = 7 rays; three-quarters shaded = 8 rays; and all shaded = 9 rays. Two of the four color types used to distinguish the females differ in males, caudal fin colors and scale marks. The male colors are coded as in females. The length of the right bar designates the status of the males in regard to color pattern. The pectoral fin of the males differs between the two species (fig. 5). The differences were coded from one to five. The length of the left bar indicates the status of the fish with regard to pectoral fin structure. When some of the figures for individual fish were plotted, they had the same ordinate and abcissa. If other tabulations are the same, the number of examples is indicated beside the circle. If other figures differ, the second type is placed above and adjoining the first. The fishes collected from Clear Creek in 1953 and 1956 are plotted together. The plots of the 1953 specimens lie immediately above a bar. Other plots without bars or above those with bars are for the 1956 specimens.

The distribution plot of males from the headwaters of Clear Creek (fig. 6a) resembles the hybrid swarms discussed by Anderson (1949). Although the plot of the six males in the 1953 collection differs from the plot of the numerous males in the 1956 collection by being in three groups of two males, I feel that the difference is more likely due to chance. Most of the plots fall into two categories, upper right and lower left. Those in the upper right are believed to represent *G.*

heterochir and those in the lower left *G. affinis*. The scattered plots between are considered hybrids. There is a pronounced gap between the plots of the hybrid and the *G. heterochir* males. The plot of only one male definitely falls in this gap. One or two more may represent backcrosses with *G. heterochir*.

The distribution plot of *G. affinis* males from the Middle Valley Prong of the San Saba River (fig. 6b) is similar to that of the assumed *G. affinis* males in the hybrid swarm. The former differs in having more individuals with five dorsal rays (away from *G. heterochir*) and having more individuals with larger heads (toward *G. heterochir*). These differences are believed to result from population or environmental differences such as those shown for members of the related *Gambusia nobilis* species group by Clark Hubbs and Springer (ms). The distribution plot of the males from the lower reaches of Clear Creek (fig. 6c) closely resembles that of both the males from the Middle Valley Prong and the assumed *G. affinis* males from the headspring of Clear Creek. No indication of introgression is noted in the downstream collection.

The pattern of the distribution plots of the females from the headwaters of Clear Creek (fig. 7a) resembles that of the males. There is no significant difference between the collection made in 1953 and that made in 1956. There are two concentrations of plots, one each for females of *G. affinis* and *G. heterochir*. The scattered intermediate plottings are assumed to represent hybrids. The gap is less marked than that found in males. This is probably due to environmental variations of color marking details.

The distribution plot of the females from the Middle Valley Prong of the San Saba River (fig. 7b) is similar to that of the assumed *G. affinis* from the headwaters of Clear Creek. Similar to the males, the females from the Middle Valley Prong differ from those in the hybrid swarm region by having more individuals with five dorsal rays and larger heads. The distribution plot of the females from the lower part of Clear Creek (fig. 7c) resembles that of both the females from the Middle Valley Prong and the assumed *G. affinis* females from the headspring of Clear Creek. No indication of introgression is noted in the downstream collection.

Discussion

A morphological study of the specimens from the headsprings of Clear Creek strongly indicates the presence of a hybrid swarm. The suspected hybrids are intermediate morphologically but definitely grade into *G. affinis* characters. Thus the intermediate hybrids (suspected F_1's) give a hybrid index similar to those given by Carl L. Hubbs, Hubbs, and Johnson (1943) for F_1 sucker hybrids. The correlation between apparently unrelated characters resembles those given by Anderson (1949) for hybrid swarms in plants.

The scarcity of specimens which would be expected to result from backcrosses of hybrids with *G. heterochir* is probably natural. Crosses

between hybrids and *G. heterochir* may be inhibited by extrinsic or intrinsic isolative mechanisms. I suspect a sterility mechanism, as the other mechanisms did not prevent crosses between the more distinct parental forms. The few individuals which are morphologically intermediate between the hybrids and *G. heterochir* may represent extreme F_2's or the result of rare backcrosses.

The hybrid swarm was present in February, 1953. In February, 1956, the constitution of the hybrid swarm had not changed noticeably. Other factors being equal, if hybrids are at a selective advantage in the environment, the frequency of hybrids should be more numerous in the later collections. No hybrids have been noted among the 17 plotted individuals from the lower part of Clear Creek or the many unplotted immature individuals from that locality. Although backcrossing with *G. heterochir* appears to be inhibited, morphological evidence indicates potential gene flow into the downstream *G. affinis* populations. Therefore, if introgression is at a selective advantage, some *G. heterochir* influence should be noticeable in downstream collections 36 months after the hybrid swarm was known to have been established.

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Abstract

A new species of poeciliid fishes, *Gambusia heterochir*, restricted to the headwaters of Clear Creek, Menard County, Texas is described. Both pectoral fins have a pronounced groove to steady the gonopodium during intromission. The new species has formed a hybrid swarm with *Gambusia affinis*. Introgression with *G. heterochir* appears negligible. Introgression is not found in near-by populations of *G. affinis*.